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RESEARCH ARTICLE

Predation risk shaped by habitat and landscape complexity in urban environments

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Abstract

1. Habitat loss and modification are hallmarks of anthropogenic ecosystems, but the consequences for ecosystem functioning and service provisioning often remain unclear. Understanding these links in cities is complicated by strong but fine-scale differences in habitat structure among green space patches, and a high variance in habitat amount across urban landscapes.
2. We used airborne laser scanning data to disentangle the effects of 3D woody habitat heterogeneity of urban home gardens, and woody habitat amount at four landscape spatial scales (50, 100, 250, and 500 m), on the predation risk of artificial sentinel prey by birds and arthropods.
3. In both predator groups, and at all the investigated spatial scales, cross-scale interactive effects between garden habitat heterogeneity and habitat amount in the urban landscape were the main drivers of predation. Risk of predation by birds was highest in heterogeneous garden habitats, but only in densely built urban landscapes where habitat amount was low to intermediate (10%–20%) at large spatial scales (250–500 m). It dropped independently of garden habitat heterogeneity when habitat amount became too low (<10%) at small (50–100 m) spatial scales. In contrast, risk of predation by arthropods mostly peaked in homogeneous garden habitats when habitat amount was intermediate (20%) at large spatial scales.
4. Our findings show that the ability of urban green space patches, such as gardens, to sustain ecosystem functions in cities mainly depends on cross-scale interactive effects with larger scale habitat amount. In birds, predation activity can increase when high patch-scale habitat heterogeneity contrasts with reduced larger scale habitat amount, suggesting concentration effects. Yet, thresholds exist under which ecosystem functioning drops independently of habitat structure.
5. *Synthesis and applications.* The potential of small-scale interventions to enhance habitat heterogeneity (e.g., by planting native trees with understorey shrubs) for

restoring ecosystem functions, such as bird predation, in urban areas is dependent on wider landscape habitat structure. Urban planning should therefore adopt a multiscale approach to sustain and restore ecosystem functions and services; a simple but still not broadly recognized finding. Airborne laser scanning is a useful tool to infer habitat structure across a hierarchy of scales in spatially heterogeneous anthropogenic ecosystems.

KEYWORDS

ecosystem functions, ecosystem services, habitat heterogeneity, light detection and ranging, pest control, trophic interactions, urban ecosystems, urban gardens

1 | INTRODUCTION

Investigating the functional consequences of land use is key to sustain ecosystem processes and their associated services, which are the goods and benefits that people draw from ecosystems (Millennium Ecosystem Assessment, 2005; Schwarz et al., 2017; Seto, Guneralp, & Hutya, 2012). The demand for ecosystem functions and services is especially high in urban areas as the world urban population is predicted to grow by 61%, to reach 6.3 billion in 2050 (i.e., 66% of all of humanity) (United Nations, 2014). Furthermore, urban land cover is, on average, expanding twice as fast as the urban population (Angel, Parent, Civco, Blei, & Potere, 2011). The importance of delivering ecosystem functions within metropolitan boundaries is therefore increasingly recognized: both to improve the health and wellbeing of urban residents, and because of the potential to reconcile urban growth with biodiversity conservation (e.g., Aronson et al., 2017; Elmqvist et al., 2015; Gaston, Ávila-Jiménez, & Edmondson, 2013).

Woody vegetation is of major importance for ecosystem functioning and service provisioning in cities (Elmqvist et al., 2015). These services can be direct, such as when street trees filter air pollutants, moderate the climate and store carbon, or indirect, by offering habitat to species that, in turn, deliver their own functions and services (Schwarz et al., 2017). Although urban woody vegetation cover has been consistently correlated to both vertebrate and invertebrate species richness and abundance across studies, it remains largely unknown how the variance in the amount and structure of the urban woody vegetation affects ecosystem functioning and service provisioning through associated organisms (Beninde, Veith, & Hochkirch, 2015; but see Philipott & Bichier, 2017).

Understanding the link between urban vegetation and ecosystem functioning is complicated by the high level of spatial heterogeneity found in urban woody vegetation across spatial scales (Casalegno, Anderson, Hancock, & Gaston, 2017). At small spatial scales, the vertical structure of woody vegetation varies strongly, ranging from patches with simplified vegetation, such as uniformly trimmed trees without understorey, to patches with complex, multi-layered vegetation filled with trees and shrubs of different sizes (e.g., Loram, Warren, & Gaston, 2008). This small-scale spatial heterogeneity is caused by contrasting green space designs and management

intensities among the numerous land owners and tenants, in combination with small property sizes (Gaston et al., 2013). At larger spatial scales, the urban landscape composition is also highly variable, but as a general pattern the amount of woody vegetation cover decreases with increasing density of built and paved land (e.g., Tratalos, Fuller, Warren, Davies, & Gaston, 2007).

One seldom studied example of an ecosystem function that may be driven by the amount and structure of woody vegetation in cities is predation or the control of pest organisms by their natural enemies (Schwarz et al., 2017). The “enemies” hypothesis predicts stronger top-down control and hence smaller prey populations driven by a more stable, diverse, and individual-rich community of (generalist) enemies in structurally heterogeneous habitats when compared to more homogeneous habitats (Muiruri, Rainio, & Koricheva, 2016; Root, 1973; but see Tschamtket et al., 2016). However, this may be counteracted as prey survival can increase with habitat heterogeneity due to lower prey detectability and accessibility (Denno, Finke, & Langellotto, 2005). Predicting the impacts of habitat loss on predation can be similarly difficult, especially in cities where diverse and novel communities can persist despite habitat loss (Aronson et al., 2014; Braaker, Ghazoul, Obrist, & Moretti, 2014; Sattler, Obrist, Duelli, & Moretti, 2011). How habitat loss impacts predator-prey interactions depends on the complex interactions between the relative vulnerability of prey and predators to habitat loss, on feeding strategies and habitat requirements of predators, and on interactions with competitors and higher level predators (Ryall & Fahrig, 2006). For example, several studies examining the effects of habitat loss have shown increasing predation rates in remaining habitat patches across ecosystems, including cities (Ferrante, Lo Cacciato, & Lövei, 2014; González-Gómez, Estades, & Simonetti, 2006; Kozlov, Zverev, & Rainio, 2017; Philipott & Bichier, 2017; Tschamtket et al., 2012; Turrini, Sanders, & Knop, 2016). This complexity is probably driven by the fact that ecosystem functions, such as predation, are often shaped by interactive effects between the small-scale habitat structure and the habitat amount of the surrounding landscape across spatial scales, which highlights the need for multiscale studies (Boreux, Kushalappa, Vaast, & Ghazoul, 2013; Tschamtket et al., 2012). The aims of our study were (a) to determine whether the predation risk of potential pest caterpillars by birds and arthropods

increases with increasing heterogeneity in the vertical woody vegetation structure of urban green space patches; and (b) to determine whether the strength of such a relationship depends on the amount of woody vegetation cover in the surroundings across four spatial scales. Finally, (c) by studying two distinct predator groups, we aimed at elucidating potential differences in predator responses to woody vegetation characteristics and spatial scales.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted this study in the city of Zurich, Switzerland (47°22'0"N, 8°33'0"E). Zurich is the core area of a metropolitan agglomeration harbouring about 1.3 million people. The municipality of Zurich currently has approximately 400,000 inhabitants and a surface of c. 92 km², placing it in the globally most frequent city size class (United Nations, 2014). Urban green spaces cover approximately 43% of settlement area (i.e., without forests, agricultural areas, and water bodies; Grün Stadt Zürich, unpubl. data).

2.2 | Study sites selection

We used home gardens (i.e., yards; hereafter "gardens") as our study sites because they are representative of urban green space due to their small size, continuous distribution along housing and urban infrastructure density gradients, and their high variance in the heterogeneity of the woody vegetation structure (Gaston et al., 2013; Loram et al., 2008). In Zurich, gardens cover approx. 11% of settlement area and 25% of urban green space (Grün Stadt Zürich, unpubl. data).

To disentangle the effects of woody vegetation heterogeneity and amount on predation risk, we randomly selected 24 gardens to include all combinations of low and high garden vertical vegetation heterogeneity and cover around each garden within a 500 m radius (Litteral & Shochat, 2017) (i.e., a stratified sampling approach; Figure 1). Each garden owner was contacted initially by letter, and thereafter by phone to arrange a garden visit. If no phone number was available, garden owners were approached personally.

The mean pairwise distance between gardens was 4.9 km (min. = 0.13 km, max. = 9.8 km). Two neighbouring gardens had to fulfil the condition of having contrasting woody vegetation heterogeneities. To control for confounding effects of garden area, the variance was kept as small as possible ($M = 382 \text{ m}^2$, min. = 107 m^2 ; max. = 791 m^2). Nevertheless, plot size was standardized by conducting the experiment and measuring woody vegetation heterogeneity in a 30-m radius (see below). We did not observe supplementary bird feeding during the experiment, as this can locally increase bird densities and negatively affect both the abundance of insect pests and ground-dwelling arthropod predators (Orros, Thomas, Holloway, & Fellowes, 2015). Finally, pesticide use in the woody vegetation, which can negatively impact pest control, was determined via a questionnaire. Pesticide

application frequency was very low among the investigated gardens (only three garden owners applied pesticides 1–3 times a year) and was therefore not further controlled in the experiment (D. Frey, unpubl. data).

2.3 | Measures of habitat amount and heterogeneity

Increasing heterogeneity in woody vegetation structure has been shown to attract insectivorous birds and arthropods to gardens (Belaire, Whelan, & Minor, 2014; Smith, Warren, Thompson, & Gaston, 2006), but it is difficult to measure this in urban areas. Mapping fine-scale differences in the amount and vertical heterogeneity of woody vegetation requires sensitive remote-sensing techniques such as airborne laser scanning (ALS) or airborne light detection and ranging. ALS-derived metrics of vegetation structure are powerful predictors of biodiversity and predator–prey interactions in natural ecosystems (Davies & Asner, 2014; Zellweger et al., 2016) and are increasingly used in urban ecology (Casalegno et al., 2017). However, ALS applications to study relationships between habitat structure and ecosystem functioning remain scarce.

As a surrogate for garden habitat heterogeneity, we used vegetation return heights from ALS data (Figure 1). We used a publicly available dataset which was acquired between March and April 2014 with an average point density of 8 per m², a footprint size of 0.2 m, and a vertical accuracy of 0.1 m. The raw data have the form of a classified point cloud including the categories: buildings, ground points, and vegetation points (data available at: <https://are.zh.ch/internet/baudirektion/are/de/aktuell/mitteilungen/gis/2015/hoehendatenzh.html>). Woody vegetation cover was defined as vegetation return heights of greater than 1 m above-ground. Heterogeneity in the woody vegetation structure was measured as the standard deviation of vegetation return heights at 30-m radius circles with the gardens centred (Muiruri et al., 2016; Zellweger et al., 2016).

Woody vegetation cover was used to estimate habitat amount and was defined as the proportion of woody vegetation in the entire ALS point cloud in each area investigated. We adopted a multiscale experimental design, in which the garden-level variables were held constant, while the spatial extent at which the habitat amount was measured was increased stepwise (Wheatley & Johnson, 2009), as the proportion of cover in 50-, 100-, 250-, and 500-m radius circles around each garden (Litteral & Shochat, 2017; Table S1). We considered multiple spatial scales because organisms and associated ecosystem processes, such as predation, are affected by factors that act at multiple spatial scales (Levin, 1992; Ryall & Fahrig, 2006). Based on previous research on urban birds and arthropods (i.e., small insectivorous birds and ground-dwelling arthropod predators) in Zurich and elsewhere we opted for a combination of several small (i.e., 50–250 m) and one large ($\geq 500 \text{ m}$) spatial scale (Braaker et al., 2014; Fontana, Sattler, Bontadina, & Moretti, 2011; Hostetler & Holling, 2000; Litteral & Shochat, 2017; Turrini & Knop, 2015).

Since urban woody vegetation can change strongly and abruptly due to cutting and planting, ALS vegetation cover data were

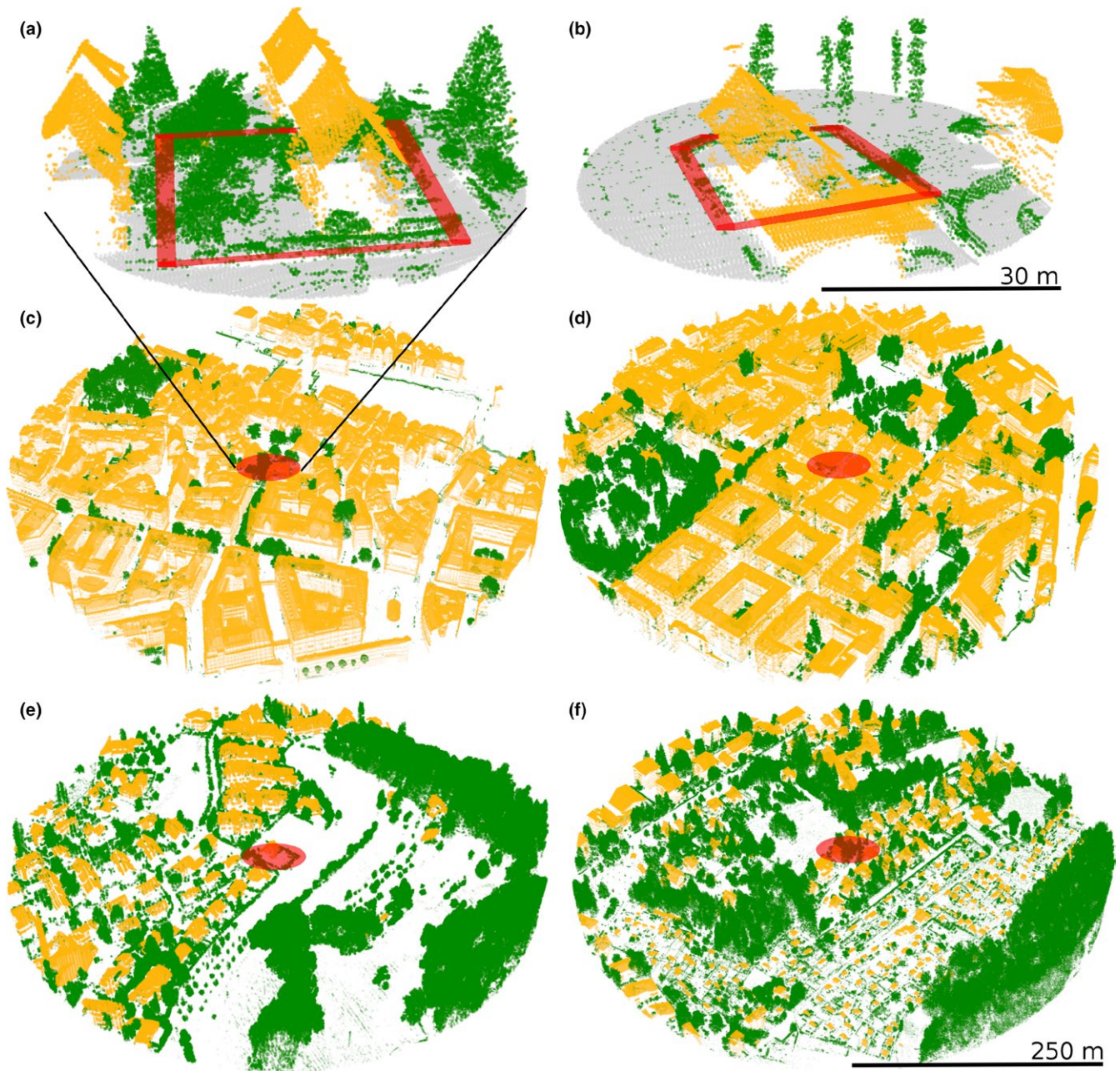


FIGURE 1 Examples of the airborne laser scanning (ALS) classified point cloud data used in our study: woody vegetation >1 m (green), buildings (orange) and ground level (grey/white). Example of gardens with high (a) and low (b) vertical heterogeneities of the woody vegetation structure (i.e., habitat heterogeneity) at the garden-patch scale (red rectangles). (c and d) It shows gardens with high and low habitat heterogeneities in 250-m scale landscapes that have low proportion ($M = 0.1$) of woody vegetation cover (i.e., habitat amount). (e and f) It shows gardens with low and high habitat heterogeneities in 250-m scale landscapes that have high habitat amount ($M = 0.3$)

compared to our own data, which were collected immediately after the experiment by manually drawing the woody vegetation cover (>1 m in height) onto aerial photographs within each garden and within a 100-m radius circle around each garden. Mappings were digitized, and woody vegetation cover was estimated with the software ArcMap (version 10.3; ESRI). Correlation coefficients between our own data and ALS-based data were high; both at garden level (Pearson's $r = 0.89$, $p < 0.0001$) and at the 100-m scale (Pearson's $r = 0.89$, $p < 0.0001$).

2.4 | Predation assessment

To quantify predation, we used artificial caterpillars as sentinel prey, which we screened for attack marks from birds and arthropods (e.g., Low, Sam, McArthur, Posa, & Hochuli, 2014). This approach has been successfully applied to reveal changes in predation risks, and thereby to infer pest-control services, across both habitat heterogeneity and land-use gradients in different ecosystems (Ferrante et al., 2014; Kozlov et al., 2017; Lemessa, Hambäck, & Hylander, 2015).

Artificial caterpillars (no edible reward for predators) were made using malleable plasticine (Staedtler FIMO® Soft; Tropical Green) that was rolled by hand into cylinders of approx. 30 × 5 mm (Low et al., 2014; Figure S1).

To standardize the substrate of the caterpillars among gardens, caterpillars were attached to bamboo rods (hereafter “artificial shrubs”), which consisted of three short (0.75 m × 23 mm) bamboo rods attached at a right angle to a single long vertical (2.25 m × 23 mm) bamboo rod. The short rods were placed at 0.5-m intervals and at 60° angles to each other to create six branches. This resulted in two branches at each of the three height classes: 0.5, 1, and 1.5 m above the ground (hereafter “caterpillar height class,” Figure S1).

Within each garden, 18 artificial caterpillars (6 per shrub) were glued to the upper side of each horizontal bamboo rod using cyanoacrylate superglue (Pattex® liquid; Henkel AG). Additionally, to assess predation activity at the ground level, two artificial caterpillars were glued on wooden chop sticks and placed below each artificial shrub, resulting in a total of 24 caterpillars per trial and a total of 1,152.

Three artificial shrubs were placed in each of the 24 gardens at a distance of at least 2 m from built structures (house or shed) and at least 4 m from one another. To standardize shrub location, we placed one shrub at each of three distance categories (hereafter “shrubs distance class”): within walking (0–0.1 m), hopping (0.1–0.7 m), and flying distance (>0.7 m) from the nearest bird's perch on a woody vegetation element. We installed the artificial shrubs at least 1 week before the start of the experiment to allow predator habituation.

Experiments were conducted between 4 and 27 May 2015, which is during the breeding season of widespread insectivorous bird species in Zurich, such as tits (*Parus* spp.), and which also parallels the peaks of caterpillar abundance in woody vegetation (Mols & Vissier, 2002; Naef-Daenzer & Keller, 1999).

The artificial caterpillars were exposed to predators for 48 hr, after which they were removed from the artificial shrubs and checked for signs of predation. We repeated this process twice for each garden with the two experimental trials being separated by at least 4 days. A caterpillar was considered to have been predated if a mark attributable to a bird, mammal, or arthropod was identified according to standard identification keys (Low et al., 2014). Marks that could not be identified in the field were examined using a binocular microscope.

2.5 | Data analysis

We used binomial GLMMs in a Bayesian framework to fit logistic regressions to the predation risk of artificial caterpillars by birds and arthropods. GLMMs were run in the software R using the package lme4 (Bates, Maechler, Bolker, & Walker, 2015). The presence or absence of predator attack marks on the caterpillar models was used as a binary response variable.

In each model, the interaction term between garden habitat heterogeneity and landscape habitat amount was included.

Similarly, since we expected nonlinear effects of habitat amount and heterogeneity on predation risk, square terms of both variables were added by using orthogonal polynomials. The final model structure, that is, whether the linear or square term of habitat amount and heterogeneity was used, was chosen based on the Bayesian widely applicable information criterion (WAIC) as implemented in the R package BLMECO (Korner-Nievergelt et al., 2015; Watanabe, 2010).

Additionally, caterpillar height class and shrub distance class were entered in the model as fixed factors. Both crossed and nested random factors with random intercepts were included in the model to account for nonindependence among observations due to repeated measurements and the nested structure of the observations in time (i.e., two trials) and space (i.e., within gardens and on artificial shrubs). All continuous explanatory variables were centred and scaled to mean zero and one standard deviation prior to analysis. Models were run separately for each spatial scale.

We used a Bayesian approach to estimate the model parameters and their uncertainty using the R package arm (Gelman & Su, 2016). To achieve this, the results from the GLMM fits were used to calculate their joint posterior distribution assuming flat prior distributions (Korner-Nievergelt et al., 2015). Mean parameter estimates were then obtained by 10,000 random samples from the joint posterior distribution, together with their 95% credible intervals, which expresses the range within the true parameter value is expected with a probability of 0.95. The latter was calculated as the 2.5% and the 97.5% quantile of the posterior distribution.

The goodness-of-fit of all models was investigated by plotting observed predation events against fitted values, while coincidence of observed and fitted values was assessed by calculating their means and the standard error of the means in suitability selected classes of fitted values. Finally, measures of explained variance were calculated for the fixed factors of each model by using the R package piecewiseSEM (Lefcheck, 2016).

To reduce the correlation between garden habitat heterogeneity and the landscape habitat amount at the 50-m scale, and hence to improve independence among explanatory variables, one garden was excluded from the analyses (Pearson's $r = 0.26$, $p = 0.23$).

3 | RESULTS

Of the 1,152 exposed caterpillars, 1,145 (99%) were successfully evaluated for predation marks. Seven caterpillars were excluded from the analysis because they had been vandalized or removed. The overall predation rate was 16.2% (approx. 8% per day).

Most of the marks were left by birds ($n = 123$, 66.5%), followed by arthropods ($n = 38$, 20.5%). Fourteen marks (7.6%) could not be unambiguously assigned to a predator class and were therefore excluded from the analysis. Bird predation marks were recorded in all 24 gardens (mean number of marks = 5.1, range = 1–19). Arthropod predation marks were recorded in 62% of gardens

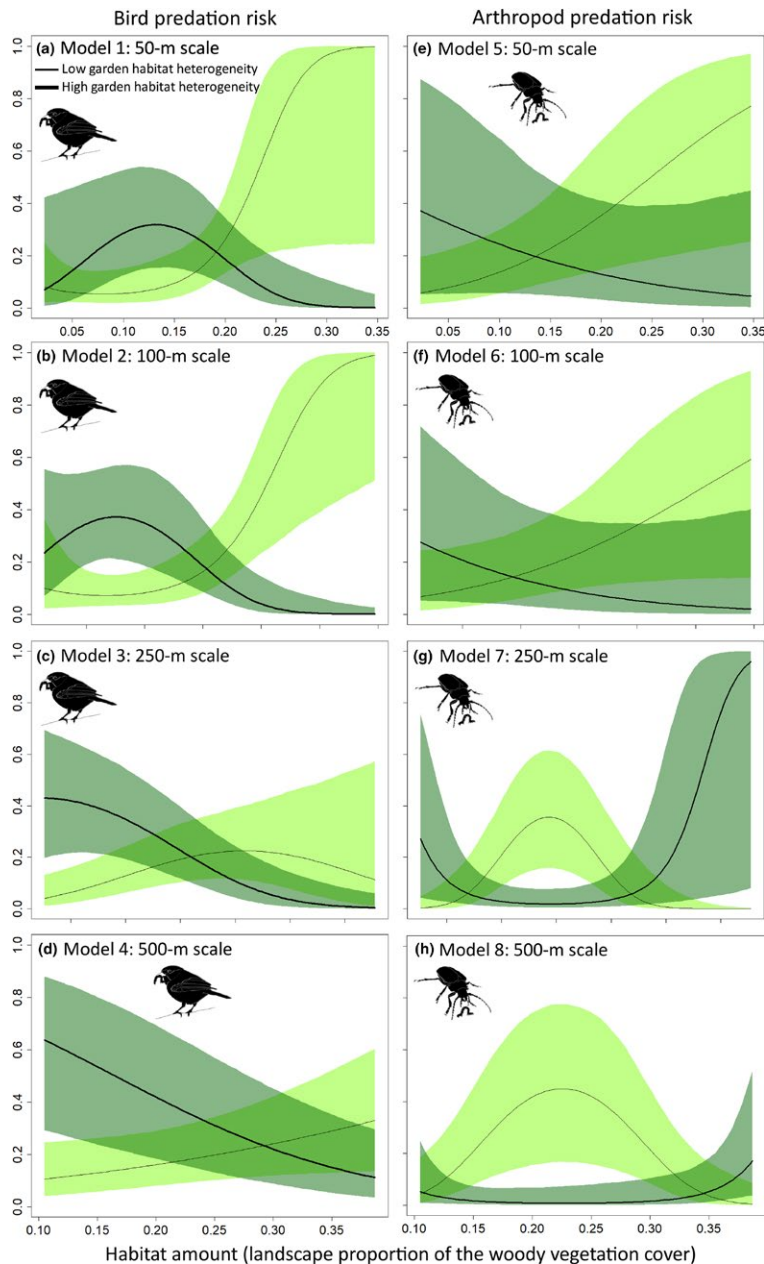


FIGURE 2 Bayesian effect plots illustrating the interactive effects between the garden habitat heterogeneity (i.e., the vertical heterogeneity of the woody vegetation structure) and the landscape habitat amount (i.e., the landscape proportion of the woody vegetation cover) on the predation risk of artificial caterpillars by birds (a–d) and arthropods (e–h). Garden habitat heterogeneity levels were taken as the 20% and the 80% percentiles of the observed standard deviations of vegetation return heights. The additional variables in the models were treated as follows: shrub distance class was held to the intermediate condition (hopping distance), while caterpillar height class was put to the highest level in birds (1.5 m) and to ground levels in arthropods, where most predation occurred

(mean number of marks = 1.6, range = 0–8). Mammal predation was not modelled due to the low number of attack marks ($n = 10$, 5.4%).

We found strong and significant interactive effects between garden habitat heterogeneity and landscape habitat amount on both risk of predation by birds and arthropods across all the investigated spatial scales (Figure 2, Tables 1 and 2). Risk of predation by birds was significantly higher only in heterogeneous gardens at low to intermediate landscape habitat amounts (10%–20%) at the larger spatial scales (250–500 m). Conversely, risk of predation by birds dropped independently of garden habitat heterogeneity when landscape habitat amount was low (<10%) at small spatial scales (50–100 m). Risk of predation by arthropods mostly peaked not only in homogeneous garden habitats when habitat amount was intermediate (20%) at large spatial scales, but

also tended to increase in heterogeneous garden habitats when landscape habitat amount was high (>30%). At small spatial scales, and in contrast to birds, risk of predation by arthropods was also strongly driven by both the linear and quadratic terms of habitat heterogeneity.

Risk of predation by birds was highest at the upper branches of the artificial shrubs, and risk of predation by arthropods was highest at ground level, but shrub distance class did not affect predation risk by neither predator community (Tables S2 and S3).

The fixed factors of the models explained on average $c. 20 \pm 2\%$ (SD) of the observed variation in the bird-predation models and $c. 30 \pm 2\%$ (SD) in the arthropod predation models, whereas WAIC values were similar across models (Table 3). Hence, the variance in explanatory power and fit among models was low (Figure S2).

TABLE 1 Parameter estimates of variables affecting risk of predation by birds based on 10,000 random samples from the posterior distributions. Significant effects, that is, credible intervals that do not include zero, are given in bold. Parameter estimates for shrub distance class and caterpillar height class are given in the additional information. G: garden habitat heterogeneity (i.e., vertical heterogeneity of the woody vegetation structure); L: landscape habitat amount (i.e., landscape proportion of the woody vegetation cover)

Parameter	Mean	2.5% CI	97.5% CI
Model 1: 50-m scale			
Intercept	-3.74	-4.57	-2.91
G	-0.12	-0.53	0.3
L	0.42	0.02	0.82
L ²	-0.1	-0.52	0.31
G × L	-0.83	-1.51	-0.14
G × L ²	-0.86	-1.63	-0.08
Model 2: 100-m scale			
Intercept	-3.8	-4.61	-2.98
G	0.14	-0.22	0.5
L	-0.07	-0.42	0.27
L ²	-0.12	-0.5	0.27
G × L	-0.88	-1.3	-0.47
G × L ²	-0.65	-1.23	-0.08
Model 3: 250-m scale			
Intercept	-3.84	-4.68	-3.02
G	0.27	-0.1	0.64
L	-0.31	-0.69	0.06
L ²	-0.42	-0.83	-0.01
G × L	-0.66	-1.1	-0.22
Model 4: 500-m scale			
Intercept	-3.8	-4.63	-2.96
G	0.21	-0.06	0.48
G ²	0.26	-0.05	0.56
L	-0.14	-0.44	0.15
G × L	-0.43	-0.7	-0.15

TABLE 2 Parameter estimates of variables affecting risk of predation by arthropods based on 10,000 random samples from the posterior distributions. Significant effects, that is, credible intervals that do not include zero, are given in bold. Parameter estimates for shrub distance class and caterpillar height class are given in the additional information. G: garden habitat heterogeneity (i.e., vertical heterogeneity of the woody vegetation structure); L: landscape habitat amount (i.e., landscape proportion of the woody vegetation cover)

Parameter	Mean	2.5% CI	97.5% CI
Model 5: 50-m scale			
Intercept	-2.34	-3.1	-1.58
G	-0.46	-0.81	-0.11
G ²	0.64	0.24	1.04
L	0.25	-0.25	0.75
G × L	-0.44	-0.86	-0.04
Model 6: 100-m scale			
Intercept	-2.52	-3.28	-1.76
G	-0.35	-0.75	0.05
G ²	0.49	0.08	0.91
L	0.08	-0.44	0.59
G × L	-0.42	-0.83	0
Model 7: 250-m scale			
Intercept	-2.68	-3.41	-1.95
G	0.17	-0.54	0.89
L	-0.09	-0.54	0.37
L ²	-0.62	-1.15	-0.07
G × L	0.16	-0.5	0.82
G × L ²	1.67	0.59	2.75
Model 8: 500-m scale			
Intercept	-2.72	-3.5	-1.93
G	-0.46	-1.05	0.12
L	-0.12	-0.63	0.39
L ²	-0.24	-0.73	0.26
G × L	0.32	-0.2	0.85
G × L ²	0.88	0.22	1.52

4 | DISCUSSION

4.1 | Cross-scale interactive effects drive predation in urban ecosystems

We found that the vertical woody vegetation structure increased predation risk of sentinel prey by birds and arthropods in urban gardens, but this depended on the extent of woody vegetation cover in the surrounding landscape matrix (Figure 2, Tables 1 and 2). Hence, the “enemies” hypothesis, which predicts strong top-down control in structurally heterogeneous habitats, may not be able to explain predation and pest control in urban habitats such as gardens on account of multiscale response interactions in

vegetation structural complexity. By contrast, the “enemies” hypothesis might be more directly relevant in comparatively spatially homogeneous ecosystems (e.g., Muiruri et al., 2016).

Our results indicate that interactive effects among habitat attributes measured at different spatial scales can play an important role in shaping ecosystem processes and services and should therefore be considered in spatially heterogeneous ecosystems such as cities (Denno et al., 2005; Goddard, Dougill, & Benton, 2010; Litteral & Shochat, 2017; Tscharntke et al., 2012). Similarly, ecosystem processes that rely on species interaction may not necessarily be negatively affected by moderate levels of urbanization, as it is frequently assumed (González-Gómez et al., 2006; Kozlov et al., 2017; Philipott & Bichier, 2017; Ryall & Fahrig, 2006; Turrini et al., 2016).

TABLE 3 The Bayesian model selection criterion (widely applicable information criterion; WAIC) and the percentage of explained variance (R^2) for the fixed effects of each model

Model	Spatial scale of investigation	WAIC	R^2
Bird predation			
Model 1	50 m	733.6	0.18
Model 2	100 m	718.7	0.21
Model 3	250 m	724.1	0.22
Model 4	500 m	730.6	0.17
Arthropod predation			
Model 5	50 m	306.9	0.31
Model 6	100 m	306.7	0.30
Model 7	250 m	300.6	0.36
Model 8	500 m	309.1	0.31

4.2 | Bird predation activity

We found evidence of elevated risk of predation by birds when the urban woody habitat amount was low to intermediate (10%–20% by area) at relatively large spatial scales (250–500 m; Figure 2c,d), but only in gardens with high heterogeneity in woody habitat structure. Such gardens represent a favourable environment for feeding, hiding, and nesting in urban contexts where such resources are otherwise scarce (Belaire et al., 2014). Similar responses have been observed in agricultural landscapes and forests where patchy resource distributions and/or habitat loss can lead to local concentrations of organisms, with functional consequences such as increased predation (González-Gómez et al., 2006; Mols & Vissier, 2002; Tscharnkte et al., 2012).

The small increase in predation observed in homogeneous garden habitats in parts of the city where woody habitat amount was high (>35%) might be explained by a combination of predator spill-over, and the high detectability and accessibility of prey in such gardens (Denno et al., 2005; Tscharnkte et al., 2012). Yet, overlapping credible intervals indicate that differences between gardens with contrasting habitat structure, if present, are small in such situations (Figure 2d). Our results indicate variation in the extent of predation by birds, subject to interactive effects in habitat complexity across scales. This has the potential to contribute to pest control, as reported by Kozlov et al. (2017) who found a stronger avian predation of herbivorous insects (leading to a foliage loss reduction of 16.5%) across 16 European cities when compared with nearby rural habitats.

At the smallest spatial scales (50–100 m), our results show that low habitat amounts negatively impact predation risk even when garden habitat heterogeneity is high (Figure 2a,b, Table 1). This effect was strongest when habitat amount fell below approx. 12% at the 50-m scale (i.e., <950 m²). This suggests that predation risks tend to scale positively with habitat size in urban areas. Urban gardens in many central and northern European cities are mostly smaller than 950 m² and tend to decrease in size with increasing urban density

(Loram et al., 2008), and thus individual gardens might not be able to support organism-mediated ecosystem services such as pest control; even when habitat quality is locally high (Goddard et al., 2010).

4.3 | Arthropod predation activity

In contrast to birds, risk of predation by arthropods was strongly affected by both (negative) linear and (positive) quadratic terms of garden habitat heterogeneity at the smallest spatial scales (50–100 m), while habitat amount alone played no role at these scales (Table 2). Previous studies, across 10 northern temperate cities on different continents, have found that local environmental conditions shape communities of ground-dwelling predatory arthropods more strongly than larger scale variables related to habitat loss (Braaker et al., 2014; Magura, Lövei, & Tóthmérész, 2010). Species of recurrently disturbed, and hence open, habitats, which are characterized by a low woody vegetation cover and heterogeneity, apparently dominate communities in northern temperate cities (Magura et al., 2010). Similarly, Lemessa et al. (2015) found increased arthropod predation in home gardens in tree-poor agricultural landscapes of Ethiopia, East Africa, yet they did not find an influence of woody habitat structure at the garden scale.

On the other hand, species closely associated with woody habitats might be more frequent at forested urban fringes (Magura et al., 2010). Indeed, at larger spatial scales (250–500 m), we found increased predation risks in structurally homogeneous, and hence open, gardens in urban contexts with intermediate habitat amount (20%), as well as in structurally heterogeneous gardens in landscapes where woody habitat amount was relatively high (>30%). Although the latter result is in line with Ferrante et al. (2014), its explanatory power is low as indicated by the wide credible intervals (Figure 2g,h). Nevertheless, taken together, such findings may suggest that two communities of ground-dwelling predatory arthropods with contrasting habitat preferences might have driven the observed pattern (Figure 2g,h).

4.4 | Management implications

Analogous to agricultural ecosystems, our results indicate that providing locally heterogeneous vertical woody vegetation structures (e.g., by planting and maintaining tall-growing native trees with understorey shrubs) to enhance ecosystem functions, such as predation by birds and arthropods, is likely to be most effective when the suitable habitat amount is neither too low (e.g., <10%) nor too high at larger landscape spatial scales (Boreux et al., 2013; Tscharnkte et al., 2012). We surmise that this is because the absence of large source habitats (e.g., forest fringes) prevents spill-over effects which might otherwise overcome small-scale differences in habitat structure, yet sufficient predators persist within the habitats distributed across the urban landscape to respond to localised habitat heterogeneity (Aronson et al., 2016). Indeed, large urban areas with extremely reduced favourable habitat cover are likely to contain a depauperate predator community that is not able to respond to small-scale management measures (Tscharnkte et al., 2012).

Since different predator groups or communities can show contrasting activity patterns with respect to woody vegetation heterogeneity, management trade-offs may exist. In moderately urbanized landscapes, providing woody habitat heterogeneity appears to more effectively favour predation by birds than by arthropods. This is probably due to the relatively lower mobility of the latter or because the size and quality of garden habitats is rarely sufficient to sustain local populations (Braaker et al., 2014; Goddard et al., 2010; Magura et al., 2010). Besides improving the size and quality of garden habitats, for instance by decreasing management intensity (i.e., decreasing pruning and mowing frequency and pesticide use) and offering more mature native woody vegetation (e.g. Sattler, Duelli, Obrist, Arlettaz, & Moretti, 2010), improving landscape connectivity by green corridors of high quality habitat could additionally increase colonization rates of gardens by such arthropod predators (Beninde et al., 2015).

Open urban habitats might benefit more immediately by interventions to enhance arthropod predation activity (Magura et al., 2010). Habitat heterogeneity other than that of woody vegetation is still relevant in such situations (Denno et al., 2005) and garden owners could enhance pest control by arthropod predators by maintaining uncut perennial and tussock forming grasses as “beetle banks” (Tschardt et al., 2012).

4.5 | Using ALS to predict ecosystem processes and services in urban ecosystems

Using high-resolution 3D ALS data, we are now able to quantify the urban woody habitat structure and amount in great detail and over large areas (e.g. Casalegno et al., 2017). This improves our ability to assess the relationships between woody habitat structure and ecosystem functions across a hierarchy of spatial scales and allows insights into cross-scale interactive effects which appear pervasive in spatially heterogeneous ecosystems such as cities (Goddard et al., 2010). Urban planning aiming at conserving biodiversity or increasing the ecological functionality of cities might profit considerably from these methodological developments. Conversely, studying ecosystem processes at single spatial scales without considering interactive effects across scales might be misleading, with potentially negative effects for maintaining and/or restoring ecosystem functions: a simple but still not widely recognized prediction. However, integrating multiple spatial scales into urban ecosystem planning also requires bridging the apparent mismatches between ecological (i.e., minimum habitat size) and social (i.e., property size) scales and boundaries, which is challenging (Gaston et al., 2013). Future studies should therefore also explore the social drivers of urban habitat structure and ecosystem functioning by including the different scales of social organization (e.g., individual, neighbourhood) and decision making (Aronson et al., 2017).

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AUTHORS' CONTRIBUTIONS

D.F., K.V., M.M., J.G., and D.H. designed the experiment; K.V. developed the artificial prey approach and guided the fieldwork; F.Z. processed the ALS data and provided valuable methodological comments; D.F. performed data analysis and wrote the paper. All authors edited the paper and approved the final version.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.h388h3g> (Frey et al., 2018).

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